

except when disturbed. In contrast, pediveligers alternated between swimming and crawling on the bottom. Periods between planktonic excursions increased through time. Pediveligers still fed while on the bottom by orienting themselves velar-side-up and creating feeding currents with their cilia. The larger pediveligers appeared to sink faster than smaller larvae, and spent most of their time on the bottom of the culture vessels. The feet of these larvae were so large (relative to velum) that they appeared to interfere with swimming.

### Larval Settlement

Pre-soaked adult shell fragments were added to three culture vessels when the first pediveligers were observed (day 12). Settlement was first observed on day 21 (12 December) when 148 spat were counted. The cumulative number of spat increased to 180 by day 23, and decreased to 163 on day 25. Mortality due to handling was the most likely cause of the decrease. The number of settlers further declined after day 25 in the settlement vessels.

Shell fragments were added to the vessels which had never had settlement substrate added on day 58, to determine if the pediveligers were still capable of settling. No settlement was observed when larval culture was terminated on day 60 even though the larvae appeared healthy, their guts were full of algae, and they were still capable of swimming.

## DISCUSSION

The population of *S. tenebrosus* on the Waikiki artificial reef spawned between 10 August and 21 September 1996. It is likely that other populations of *S. tenebrosus* in Māhala Bay spawned during this period because the gonads of all the animals sampled from other areas in the Bay on 23 September were empty. Temperature is therefore circumstantially supported as a field spawning cue for *S. tenebrosus* since warming and spawning occurred within the same 3-week period. Many other pectinaceans have been observed to spawn during summer/fall annual temperature maxima (Bonardelli et al., 1996; Tammi & Turner, 1997; Villalejo-Fuerte & Garcia-Dominquez, 1998; Baqueiro & Aldana, 2000).

The spawning cue that induced adults to spawn in the lab is unclear since the animals were both injected with serotonin, and warmed. Serotonin injections did not induce spawning within 2 hours, but the serotonin injections in combination with warming may have triggered spawning. However, warming alone may also have triggered spawning. Warming is supported as a spawning cue in the lab because, in this study, natural populations spawned during a warm event, and other pectinaceans spawn in response to warming in the lab (e.g., Monsalvo-Spencer et al., 1997). As a caveat, the results of other lab spawning studies suggest that cold-shock is an effective spawning cue for some tropical pectinaceans (Velez et al.,

1990; Chaitanawisuti & Menasveta, 1992); cold-shock was not attempted in this study. Further work is needed to determine if warming is a consistent spawning cue for *S. tenebrosus* in the lab and for natural populations.

Larval development of *S. tenebrosus* from fertilization to the straight-hinged stage (first feeding stage) occurs within 24 hours. This rate of development during early stages is similar to that reported for other species of tropical pectinaceans (Bellolio et al., 1993; Chaitanawisuti & Menasveta, 1992) and faster than some temperate pectinaceans (Strathmann, 1987). The period that *S. tenebrosus* takes to develop to the pediveliger stage is shorter (by a few days) than other tropical pectinaceans (Belda & Del Norte, 1988) and up to 2 weeks shorter than temperate pectinaceans (Beaumont & Budd, 1982; Strathmann, 1987).

The results of this study suggest that the minimum pre-competent period for larvae of *S. tenebrosus*, cultured at 22.0° to 24.0°C, is approximately 21 days. The utility of this laboratory-derived period to estimate natural pre-competent periods is arguable, given that temperature and food availability in the field is variable. The pre-competent period is likely to decrease with increasing temperature, and increase with decreasing food availability. The seasonal range of Oahu surface coastal water is 22.0° to 28.5°C (personal observation), and veligers of *S. tenebrosus* occur in the plankton year-round (personal observation). Therefore, *in-situ* pre-competent periods may be less than 21 days during spring, summer, and fall, when the temperature is greater than 24.5°C, and longer during winter when the temperature is lower. It is likely that natural populations of larvae are exposed to lower food concentrations than the larvae cultured in this study. Therefore, the pre-competent period of natural larvae may be longer than 21 days any time of year.

More than 100 pediveligers that never had substrate added to their vessels survived for the entire 60 day culture period. These pediveligers appeared healthy when culture was discontinued, and probably would have survived longer. The effect of delayed settlement on dispersion is questionable since older and larger pediveligers appeared to swim for shorter periods with increasing culture period. Events such as periods of large swell may increase the dispersion of long-lived, bottom-dwelling pediveligers through resuspension, which would extend the period that these larvae are subject to dispersal. The fact that the larvae that were prevented from settling until day 58 did not immediately settle when substrate was added to their culture vessels suggests that the period that larvae can delay settlement and successfully settle is limited to less than one season.

The results of this study indicate that *S. tenebrosus* is capable of completing its reproductive cycle in the lab within 60 days. Therefore, natural populations of *S. tenebrosus* in Hawaii likely reproduce more than once per year. A 60-day reproductive cycle for pectinaceans is not

unusual since the reproductive cycle of *Argopecten ventricosus*, a hermaphroditic pectinacean, was observed to be as short as 27 days in the lab (Monsalvo-Spencer et al., 1997). Natural populations of many other pectinaceans spawn more than once per year (Baquero & Aldana, 2000).

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## Mass Exhumation and Deposition of *Mulinia lateralis* (Bivalvia: Mactridae) on an Intertidal Beach, St. Catherines Island, Georgia, USA

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**Abstract.** Episodic events which affect populations of marine invertebrate species are rarely documented. We report the catastrophic mass exhumation and deposition of a large aggregation of adult bivalves (*Mulinia lateralis* [Say, 1822]) to a suboptimal habitat on a sandy intertidal beach of St. Catherines Island, Georgia, USA. The displaced population impacted a large area (7000 m<sup>2</sup>) of the beach and consisted of similar-sized clams (~13 mm mean shell length). We suggest that the exhumation could have been a result of storm-induced shear stress, an hypoxic event, or other environmental stress on the individuals. Events of this type could have important implications for population dynamics and cohort distribution, fisheries predictions and harvests, and interpretation of fossil assemblages.

### INTRODUCTION

On 4 October 1993 we observed a large patch of *Mulinia lateralis* (Say, 1822), the dwarf surfclam, in the intertidal zone on South Beach, near Flag Pond, St. Catherines Island, Georgia (Figures 1, 2). This was a notable occurrence because most adult infaunal bivalves are sedentary, moving long distances only as larvae or stochastically by rafting with eroded substrata, and because *Mulinia lateralis* are normally found subtidally.

*Mulinia lateralis* typically occurs in near-shore environments along the Atlantic and Gulf coasts of the United States and can be present subtidally in very dense infaunal aggregations. *Mulinia lateralis* can occur episodically and in very high densities (21,000 m<sup>-2</sup>) subtidally (Santos & Simon, 1980). Santos & Simon (1980) found that an ephemeral population of *M. lateralis* in Tampa Bay, Florida had an average density of approximately 5700 m<sup>-2</sup> when present. Montagna et al. (1993) reported a population in Laguna Madre, Texas with densities up to 800 m<sup>-2</sup> soon after recruitment in the spring, and low densities (< 100 m<sup>-2</sup>) for the majority of the year. Walker & Tenore (1984) found that the density varied with habitat in Wassaw Sound, Georgia. Populations with the highest average density were in sandy mud (10,161 m<sup>-2</sup>), whereas mud and sand habitats had lower densities (277 m<sup>-2</sup> and

263 m<sup>-2</sup>, respectively), but all population densities fluctuated widely. *Mulinia lateralis* populations have not been reported occurring intertidally in such dense live aggregations as we report, and apparently this aggregation was exhumed and deposited.

### OBSERVATIONS

The site of the *Mulinia lateralis* accumulation, South Beach, is a medium-energy (silty-sand) beach on the seaward side of St. Catherines Island. St. Catherines Island is a relatively pristine environment as there is little human activity on the island except in a research and conservation compound on the north-west (leeward) portion. Mean tidal amplitude is approximately 2.5 m. High tides were increasing toward a maximum, from +2.1 to +2.6 m mean low water at the time of observation, and this condition had been present during the 5 days preceding our observations. There had been no significant rainfall since 27 September 1993 when 0.2 cm fell (as recorded on Sapelo Island, Georgia). Wind velocity recorded on Sapelo Island had remained below 10 m/sec for the month prior to our observation and reached a velocity of 8.36 m/sec on 30 September 1993.

To quantify the extent of the exhumed population in the intertidal zone, we sampled at ebb tide along a tran-



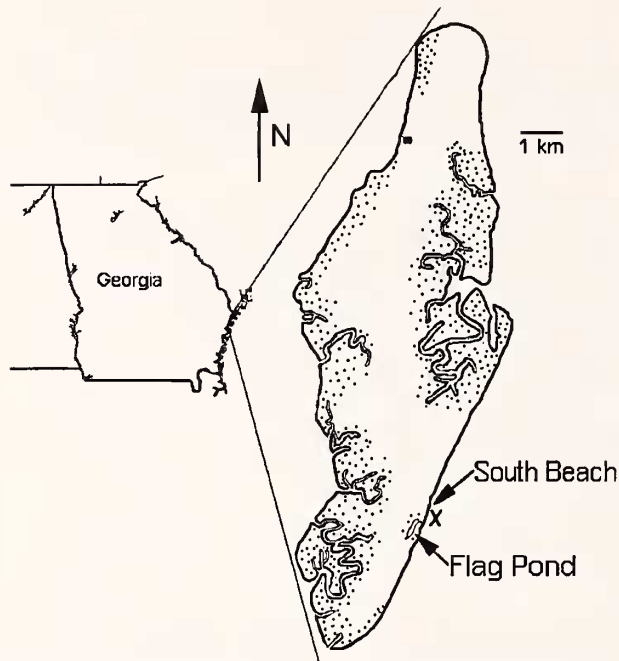


Figure 1. Diagrammatic map of St. Catherines Island, Georgia. Salt marsh is indicated by stippling. The study site is indicated by an X.

sect extending from the wrack line, approximately 80 m landward of the low tide line, to a tide level present 1 hour before maximum low tide. We used circular quadrats of 30 cm diameter (area = 706.5 cm<sup>2</sup>) to sample at 2 meter intervals along the transect. All live and dead clams present to a depth of 7 cm were collected. The number of live and dead clams within each quadrat was counted. Where clams were present on the surface, as well as buried, the ratio of surface to subsurface clams was noted.

The exhumed clams covered a large area of the beach (Figure 2). The surface aggregation extended approximately 17 m north to south and 14.5 m east to west (246.5 m<sup>2</sup>), whereas the sub-surface accumulation was much larger and extended approximately 87 m north to south from the high intertidal into the subtidal zone (7000 m<sup>2</sup>). A large, but unquantified, traction load of live and dead clams also was present in the outgoing tidal swash zone.

Clams occurred on the surface midway between the swash zone and the wrack line, 24–72 m seaward from the high intertidal zone (Figure 3). Within this zone, the greatest density of exhumed clams occurred between 42 and 52 m from the high intertidal zone. The highest density of live clams occurred at 46 m (23,227 live clams m<sup>-2</sup>; Figure 3). Dead shells were much less abundant, but their distribution paralleled that of the live clams, possibly indicating passive transport or post-depositional mortality. Live clams composed 78.7% of all shells collected. Between 42 and 52 m from the upper intertidal zone, the surface shells (75%) outnumbered the buried shells (Fig-



Figure 2. *Mulinia lateralis* exposed on South Beach, St. Catherines Island, Georgia on 4 October 1993. The infaunal population extends from high to low tide lines, while the surface clams are aggregated between 42 and 52 meters from the high tide line. *Anadara ovalis* and *Busycon* species are also present. Scale bar represents 1 meter.

ure 4), but there were no differences in the proportions of dead and live clams in these samples. The mean length of all clams was  $12.84 \pm 1.17$  mm (Figure 5) with no significant ( $P < 0.001$ ) difference between dead and live clams. The majority of live clams examined were sexually mature with ripe gonads.

#### ACCUMULATION ORIGIN

The mass exhumation of *Mulinia lateralis* reported here was notable because of the limited spatial distribution and because of the very high density of clams involved. Levinton (1970) reported large aggregations of dead valves of this species in Long Island Sound and Narragansett Bay, Rhode Island, and discussed the significance of such dense death assemblages for the fossil record. He suggested that those assemblages were the result of post-mortem transport. Other bivalves, notably the surf clam *Spisula solidissima* (Dillwyn, 1817), were observed washed up on New Jersey beaches near their subtidal populations; however, the majority observed during this event were dead or dying (Boyajian & Thayer, 1995). The authors described a storm-deposit of surfclams, and suggested mechanisms of exhumation and deposition, including the hypothesis that storms could remove overlying sediment, increasing the likelihood of subsequent population excavation and size-selective excavation and deposition. Rees et al. (1977) also noted storm-induced strandings of several bivalve species along the coast of North Wales. They stated that wave activity could be a factor in the maintenance of soft bottom benthic associations in near-shore waters.

Although no storms had occurred along the Georgia coast in the month prior to the exhumation event, large waves remain the likely mechanism transporting these

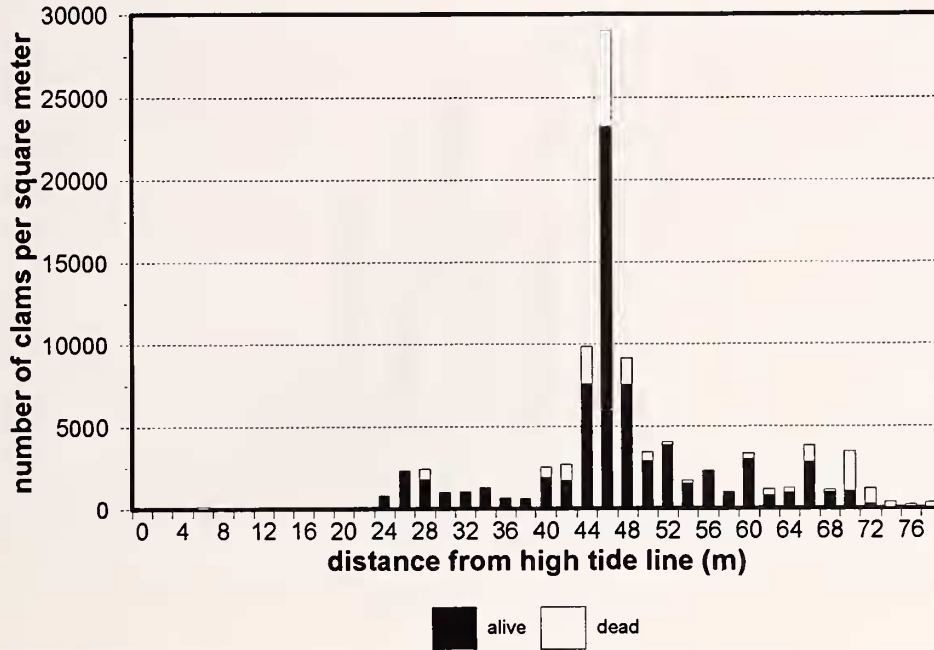


Figure 3. Frequency distribution of *Mulinia lateralis* occurring in the intertidal zone of South Beach, St. Catherines Island, Georgia, on 4 October 1993.

adult megafaunal clams so high into the intertidal zone. Palmer (1988) discussed the importance of passive transport of meiofaunal species and concluded that for such small organisms it is a fairly important mechanism of dispersal of both adults and juveniles. Passive wave-in-

duced movement of any organism involves shear stress, and the larger the organism, the higher the shear stress needed to initiate movement (i.e., erosion) (Denny, 1988). Therefore, a relatively large shear stress, present in large waves or in storm-induced seas, was likely needed to lift

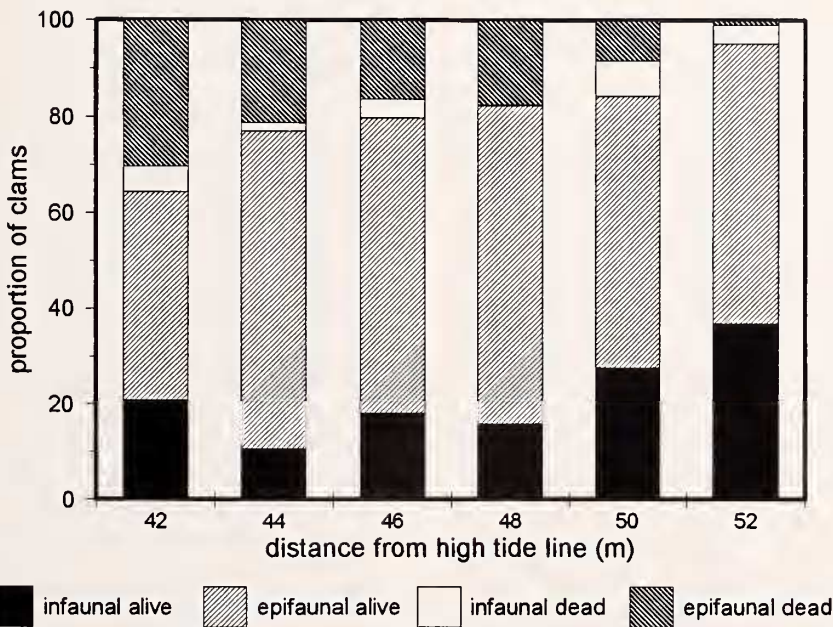


Figure 4. Percent contribution of dead and live *Mulinia lateralis* to surface and infaunal populations occurring in the intertidal zone of South Beach, St. Catherines Island, Georgia, on 4 October 1993.

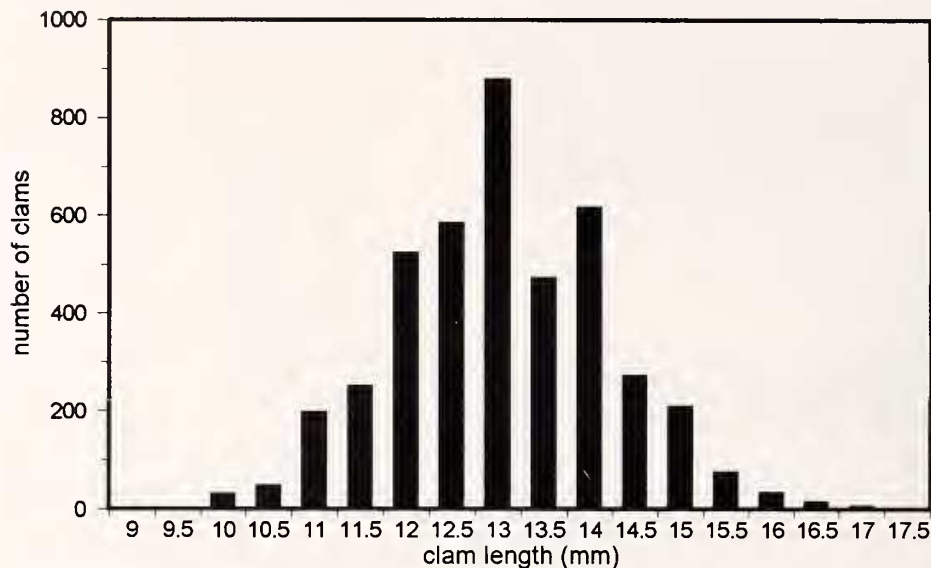


Figure 5. Length-frequency distribution of *Mulinia lateralis* occurring in the intertidal zone of South Beach, St. Catherines Island, Georgia, on 4 October 1993.

and initiate movement of these fairly large clams. Although tidal energy represents a potential source of movement of the clams, the tide prior to the exhumation event was not unusual in magnitude. Other mollusks, including the blood ark (*Anadara ovalis* [Bruguère, 1789]) and whelk species (*Busycon* species), which were much larger (5+ cm length) than *Mulinia lateralis* occurred in patches along the beach on the day of observation, possibly indicating community-wide disturbance, rather than a monospecific disturbance.

*Mulinia lateralis* has relatively short siphons that require it to remain near the surface to feed (Chalermwat et al., 1991). Therefore, passing of a shrimp otter trawl net over the population (commercial shrimp trawling is important in Georgia, especially during summer months, and occurs frequently in the ocean waters within sight of St. Catherines Island beaches) could facilitate the excavation of large numbers of individuals. Exposure on the sediment surface, combined with the strong tidal flow characteristic of the region or wind-driven mixing, could transport the clams into intertidal areas and deposit them. There were many *M. lateralis* still in suspension and buried just beneath the surface in the swash zone (approximately 1400 clams m<sup>-2</sup>), indicating that the depositional event may still have been occurring, or that the population was being actively reworked at the time of observation.

Bivalves will often move close to or onto the surface when stressed by extremes in environmental conditions, such as low salinity or hypoxic events, possibly enhancing the likelihood of exhumation and transport of a population (Cleveland, 1991; Richardson et al., 1993). We have no records of subtidal environmental parameters,

such as salinity and temperature, for this area, and therefore can only speculate as to what caused the observed phenomenon. It seems unlikely that these clams were transported a long distance before being deposited and were probably from an area relatively nearshore in the vicinity of South Beach. *Mulinia lateralis* typically inhabits sandy-mud substrata (Walker & Tenore, 1984), which are abundant in areas around St. Catherines Island. Most likely, a cojacent population was exhumed and displaced.

#### EFFECT ON POPULATION DYNAMICS

Events similar to the one observed and described could effectively entrain an entire population of clams and move it to a new site. If the exhumation is extensive, the entire population could be deposited onshore, resulting in high mortality by the stress of dislodgment, desiccation, and extreme temperature. *Mulinia lateralis* is an opportunistic species that colonizes areas quickly (Levinton, 1970), and therefore, exhumation of this type, prior to a major recruitment event, could have short-lived effects on the overall population dynamics.

Previous observations of bivalve movement have shown that some large adults, such as the northern quahog *Mercenaria mercenaria* (Linnaeus, 1758), can be entrained in high energy waters leading to an adjunct mode of dispersal beyond larval propagules (Prezant et al., 1990; Rollins et al., 1992; Boyajian & Thayer, 1995). Also, vagrant bivalves, such as *Donax* species, move regularly across a habitat (Ansell & Truman, 1973). Passive transport resulting in colonization of a habitat can be an important mechanism for population dispersal and estab-